



Research article

Assessing distributions of two invasive species of contrasting habits in future climate

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ARTICLE INFO

Article history:

Received 19 May 2017

Received in revised form

4 December 2017

Accepted 20 December 2017

Available online 28 December 2017

Keywords:

Invasion

Climate change

Range size

Niche

Species distribution modelling

ABSTRACT

Understanding the impact of climate change on species invasion is crucial for sustainable biodiversity conservation. Through this study, we try to answer how species differing in phenological cycles, specifically *Cassia tora* and *Lantana camara*, differ in the manner in which they invade new regions in India in the future climate. Since both species occupy identical niches, exploring their invasive potential in different climate change scenarios will offer critical insights into invasion and inform ecosystem management. We use three modelling protocols (i.e., maximum entropy, generalised linear model and generalised additive model) to predict the current distribution. Projections are made for both moderate (A1B) and extreme (A2) IPCC (Intergovernmental Panel on Climate Change) scenarios for the year 2050 and 2100. The study reveals that the distributions of *C. tora* (annual) and *L. camara* (perennial) would depend on the precipitation of the warmest quarter and moisture availability. *C. tora* may demonstrate physiological tolerance to the mean diurnal temperature range and *L. camara* to the solar radiation. *C. tora* may invade central India, while *L. camara* may invade the Western Himalaya, parts of the Eastern Himalaya and the Western Ghats. The distribution ranges of both species could shift in the northern and north-eastern directions in India, owing to changes in moisture availability. The possible alterations in precipitation regimes could lead to water stress, which might have cascading effects on species invasion. *L. camara* might adapt to climate change better compared with *C. tora*. This comparative analysis of the future distributions of two invasive plants with contrasting habits demonstrates that temporal complementarity would prevail over the competition.

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1. Introduction

1.1. Climate change and invasive species

Invasive species may have unique responses to climate changes, with invasive potential being highly species-specific (Pearson et al., 2002). Invasive species increase the vulnerability of ecosystems to other climate-related stressors (Burgiel and Muir, 2010). Reductions in the ranges of species are likely to occur with the global rise in temperature, when physiological activities of plants decelerate after a thermal optimum. The plant phenology and capacity of individual species to resist adverse changes in climate are crucial

for their invasion success in the future climate. According to Broennimann et al. (2006), by 2050, annuals are less likely to be affected by climate change than are perennials. The availability of global climate data offers an opportunity to predict the future distribution of species under moderate to extreme climate change scenarios. According to the Intergovernmental Panel on Climate Change (IPCC) Protocol, the A1B scenario is moderate with high economic growth. It assumes balanced use of energy resources and efficient technology. In contrast, the A2 scenario is seen as extreme with a rapid population growth and low per capita income, wherein technology is assumed to change at the regional level with poor economic development (Solomon et al., 2007).

1.2. Habits and invasion capabilities of species

Complementarity is a property of reciprocating in which some aspects of a set of objects (e.g., species) differ from those of the

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objects of another set (Williams, 2001). It encompasses interactions among two or more species in space and time (Ewel, 1986; Fargione and Tilman, 2006). Exotic invaders with superior resource use capabilities dominate. Such invaders are introduced mostly in places where there are anthropogenic disturbances. These species use the available resources efficiently and change the properties of native ecosystems (Vitousek, 1986). They alter the species composition and reduce the abundance of native species (Hejda et al., 2009). With their superior growth potential and efficient dispersal mechanism, these invaders establish themselves in native ecosystems rapidly (Sharma et al., 2005). Species with different phenological cycles (e.g., annual or perennial) uses resources asynchronously, by space partitioning and different growth periods (Gulmon et al., 1983; Qin et al., 2003). Annuals senesce after each growing season by exhausting their growth pool and perennials need resources throughout their life cycles (Leffler and Ryel, 2012). The limited availability of soil nitrogen and moisture inhibits the growth of perennials much more significantly than it does that of annuals as the latter remain active for a short span of time (Blank, 2010; Leffler and Ryel, 2012).

1.3. Habits of target species

Cassia tora (Fabaceae) and *Lantana camara* (Verbenaceae), two widespread species, were selected for the present study. They have similar life forms and common origins, but they differ in life cycle patterns. *C. tora* is an annual and *L. camara* is a perennial. *C. tora* is native to the Old World, eastwards to Polynesia, and it is found in open lands and crop fields in South-East Asia and in the south–west Pacific (Singh, 1968). It has anti-oxidant, anti-microbial, anti-proliferative, anti-genotoxic, hepato-protective, hypolipidemic, anti-inflammatory, anti-diabetic and immune-stimulative properties (Shukla et al., 2013). Its seeds are used as a coffee substitute. Each *C. tora* plant produces an average of 643 seeds. The species exhibits effective seed dormancy. Seed germination sets in with pre-monsoon rainfall in June and reduces during the dry–months (October–November) of winter (Gupta and Yadav, 2007). The seed germination can be delayed due to low temperatures, which reduces the permeability of the seed coat; warm climatic conditions favour its distribution (Singh, 1968). Seeds of *C. tora* are dispersed over short distances by water and animals.

L. camara is a species native to Central and South America. It has become naturalised in more than 60 countries between latitudes 35°N to 35°S (Day et al., 2003). It has anti-bacterial, anti-microbial, anti-inflammatory, anti-tumour, and anti-AIDs properties (Sharma et al., 2007). The species was imported to India as an ornamental plant in 1809, and now, it is a common weed of dry forests, *jhum* (slash-and-burn) fallows, and pastures (Sharma et al., 2005). *L. camara* plant produces an average of 10,000–12,000 seeds per year, and these seeds germinate throughout the year when the soil moisture, light, and temperature are sufficient (Kohli et al., 2006; Gentle and Duggin, 1997). Often, water logging and soil salinity impede the growth of this species (Swarbrick et al., 1998). Birds facilitate the long-distance dispersal of *L. camara* (Cronk and Fuller, 1998).

1.4. Species distribution modelling

Several species distribution models (SDMs) can be used to describe individual species' responses to the changing climate, and to describe the suitability of habitats for invasive species over a geographic space (Richardson et al., 2000; Kriticos et al., 2003; Jiménez-Valverde et al., 2011). SDMs use presence or presence–absence data. In case true absence data are not available, pseudo-absence data or randomly simulated background data are

often used by different models. The generalised linear model (GLM) is a widely-used, simple, parametric linear regression technique used for predicting the distributions of invasive species (Nelder and Baker, 1972; Fitzpatrick et al., 2007). Generalised additive model (GAM) is an extension of this model, but it fits a non-parametric and nonlinear relation between species and the environment (Yee and Mitchell, 1991). The Maximum Entropy (Maxent) model is a non-parametric and nonlinear machine learning technique, used for mapping habitat suitability in the future climate (Phillips et al., 2006; Hijmans and Graham, 2006). Like GAM, Maxent can quantify complex species–environment relationships. Both the regression models calculate occurrence probabilities, whereas Maxent estimates the relative probabilities of the species distribution.

In the present study, we assessed the invasive potential of species with different phenological cycles to understand the impacts of climate change on their distributions. We took advantage of the fact an extensive floral database is available to quantify the invasion potentials of *C. tora* and *L. camara* in moderate and extreme climate change scenarios. The spatiotemporal changes in the range sizes were mapped to compare the occupation of the native niches by the two species. Our hypothesis was that *C. tora*, with its short life span, would be more sensitive to diurnal variations, while *L. camara* would be sensitive to seasonal variations. The two species are likely to compete for resources as their peak growing seasons overlap. We also tried to answer the question; do differences in phenological cycles define the invasion success of species under climate change scenarios?

2. Materials and methods

2.1. Data preparation

We pooled the species location points, collected through stratified random sampling, by the project 'Biodiversity Characterization at Landscape Level' (<http://bis.iirs.gov.in>) project, a national level assessment (Roy et al., 2012). The sample design involved a nested quadrat of dimensions 20 m × 20 m laid for trees or lianas, which accommodated two 5 m × 5 m quadrats at the opposite corners for sampling shrubs. The sample plots were selected to accumulate species composition data across vegetation strata, with a minimum sampling intensity of 0.001–0.002% (Roy et al., 2012). We considered a total of 1684 and 2526 location points for *C. tora* and *L. camara*, respectively (Fig. 1). We gathered 35 climate data layers from CliMond data at a resolution of 10' (Kriticos et al., 2012), and masked these layers to India's boundary with WGS84 projections using ArcGIS 10. The multicollinearity of the predictor variables was tested using the package 'usdm' in R (Naimi, 2015). We selected variables with VIF (variance inflation factor) < 5 and correlation < 0.75 for modelling.

2.2. Modelling

The regression models (GLM and GAM) were fitted with the binomial distribution (link = 'probit') using the present point locations, and absences selected randomly from within the area of interest. We used simulated pseudo-absences data after 10,000 randomisations, giving equal weights to presences and absences (Barbet-Massin et al., 2012). The importances of the variables were examined using the package 'caret' in R (Kuhn, 2016). Similarly, we selected 10,000 background points for the Maxent model that did not include actual occurrences. The extrapolation of the simulations of the model was restricted to India's boundary to maintain a similar correlation structure across the geographical space (Jiménez-Valverde et al., 2009). We prepared a bias file by selecting background points from the areas of present locations. Using Arc

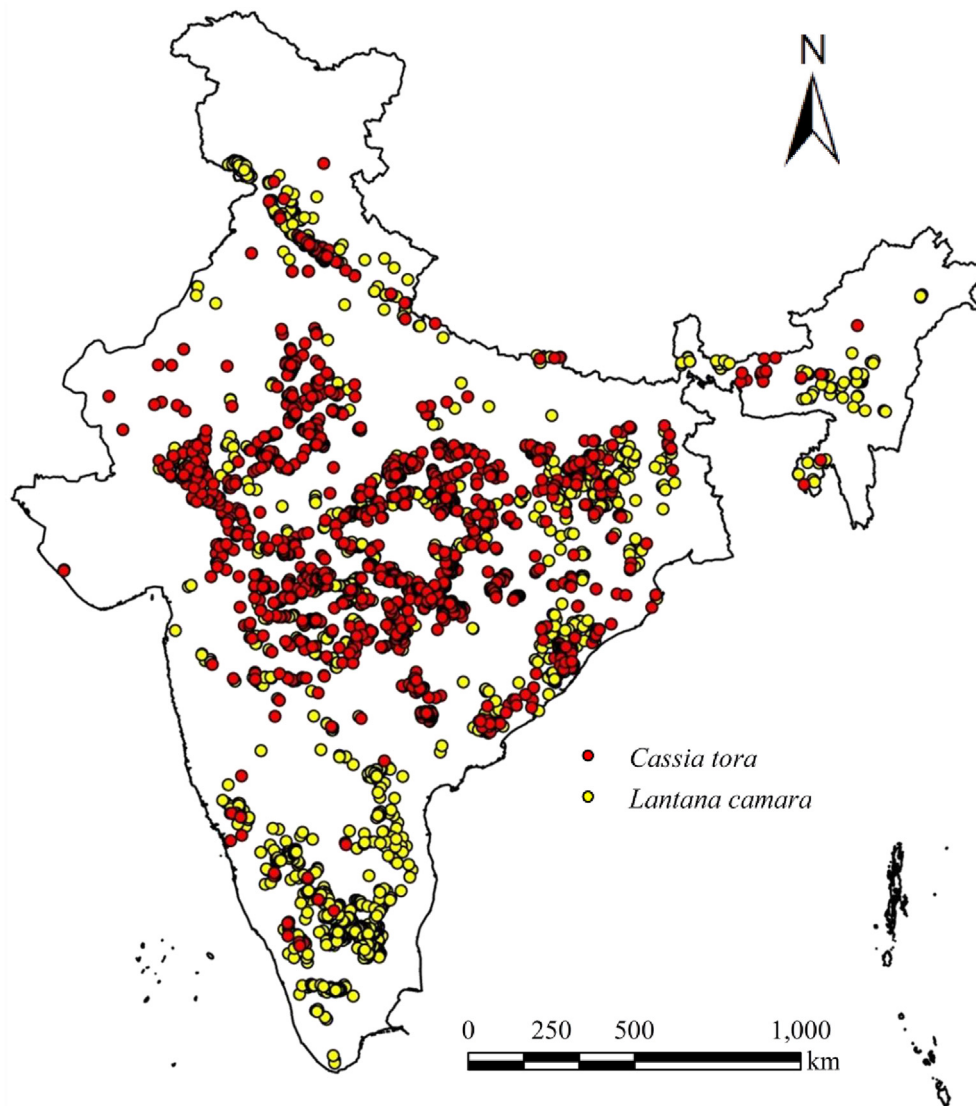


Fig. 1. Spatial location points of *Cassia tora* and *Lantana camara* in India utilised in the present study.

Toolbox, we prepared the vector layer from the states of the current locations and rasterised the polygon with the same extent, snap raster, and cell size of the predictors. The 'Con' function of raster calculator assigned '1' to all the selected states and a 'No data' value everywhere else (Young et al., 2011). The default jackknife method is used to compare the significances of the predictors. We also used the package 'phyloclim' in R to test the niche equivalency and niche similarity of the two species by Maxent model diagnosis (Heibl and Calenge, 2015). The D value and I value were derived after 100 randomisations, i.e., a sufficient number of randomisations to reject the null model with a high confidence value (Warren et al., 2008). The niche similarity was examined at the 95% confidence level to compare their similarities and differences in the geographical niche space.

2.3. Model evaluation

The input data are crucial for using SDMs. Even with scientifically designed floral data, biases may persist due to in-exhaustive sampling from the environment, and therefore, it is essential to correct bias for model optimisation. Several bias correction

measures are employed, e.g., point-wise distance sampling, wherein the test (presences and absences) and train presences are separated by assigning appropriate intervals. We prepared a bias-free sample by fixing the sample sorting bias index at 1 or close to 1 (Hijmans, 2012). We set a threshold distance of 0.33 was set to specify a fair distance between the presence and absence points. No repetition was allowed for the site selection of test absences. We evaluated the models were evaluated using both biased and bias-corrected test samples, and we compared the results with those of the null model. We performed all statistical analyses using R Version 3.1.1 (R Core Team).

2.4. Mapping species distribution

We transformed the ASCII maps derived using the Maxent model with an equal area WGS84 projection. We assigned a 10-percentile training presence logistic threshold to delineate the areas of habitat suitability (Phillips and Dudík, 2008; Young et al., 2011). A habitat suitability map offers a conservative estimate of the species' tolerance to each variable, accounts for environmental complexities, and produces ecologically significant outputs (Brito

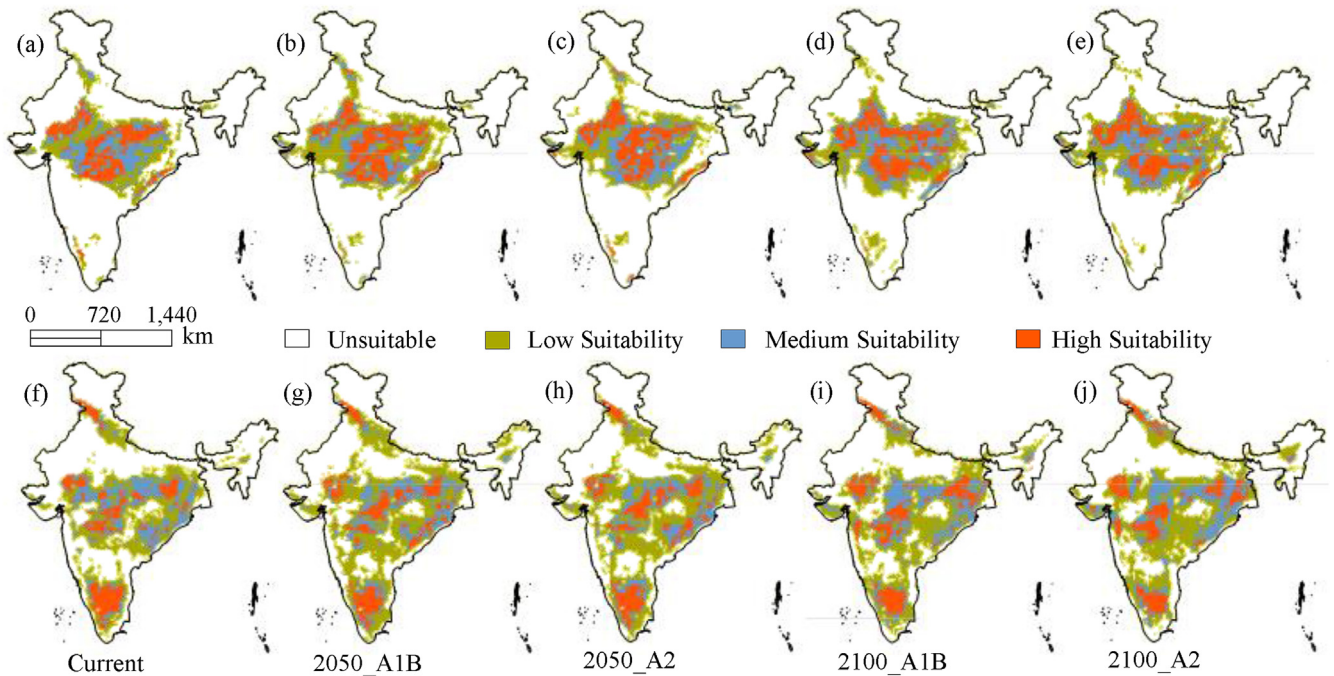


Fig. 2. Potential distribution maps of (I) *Cassia tora* (a–e) and (II) *Lantana camara* (f–j); Predictions made for the current condition (a and f) are projected for both moderate (A1B) and extreme (A2) climate change scenarios of 2050 and 2100. The distribution of *C. tora* may be localised to the central regions, while *L. camara* may be widespread over India.

et al., 2008; Lobo et al., 2008). The relative probability values above the threshold were considered suitable. We classified the suitable areas further as areas of low (up to 0.4), medium (0.4–0.6) or high (>0.6) probability of distribution (Fig. 2). We subtracted the habitat

suitability maps of the current condition from the projected maps of the future climate (for the years 2050 and 2100) to assess the changes in the range sizes under climate change scenarios (Fig. 3). We compared the expansion and reduction of range sizes using

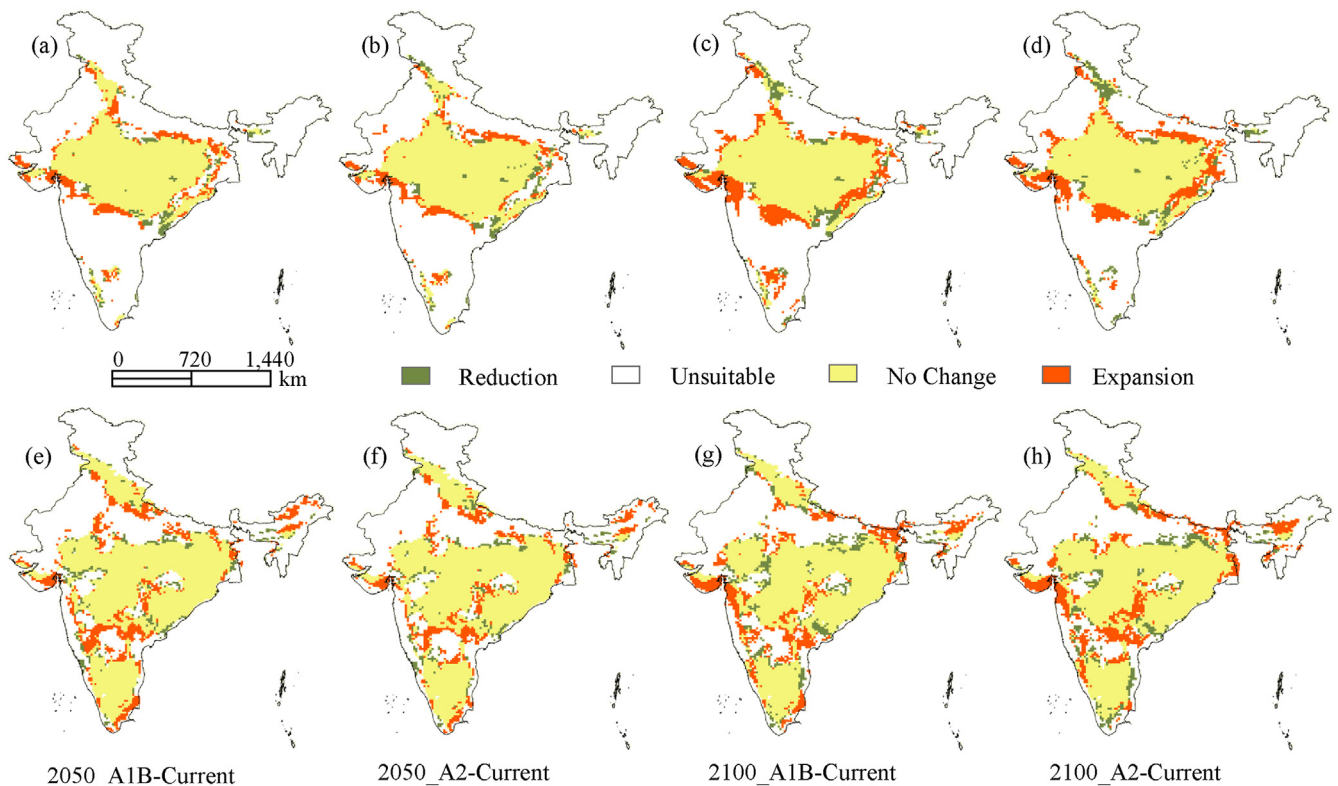


Fig. 3. Range shift maps of *Cassia tora* (a–d) and *Lantana camara* (e–h) in moderate (A1B) and extreme (A2) climate change scenarios for the year 2050 and 2100; Relative range shifting could be mostly along boundaries of the current species distribution.

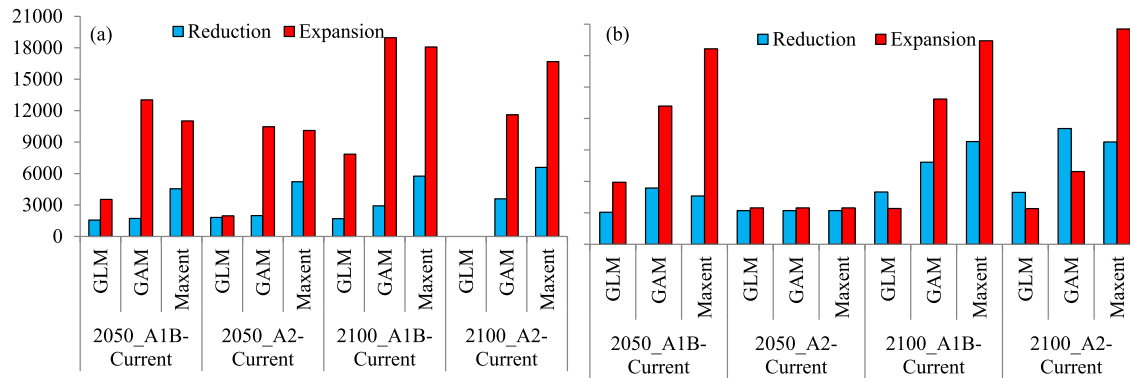


Fig. 4. Predicted changes in range areas (km^2) in distributional ranges of (a) *Cassia tora* (b) *Lantana camara* in moderate (A1B) and extreme (A2) climate change scenarios for the year 2050 and 2100; Range expansion could be more than range reduction. **Abbreviations:** GLM = generalised linear model, GAM = Generalised additive model, Maxent = Maximum entropy model.

different modelling protocols (Fig. 4). We performed the pre-processing and organisation of environmental data using ArcGIS 10.

3. Results

3.1. Model building

We selected the eight variables that were the least correlated (<0.75) for modelling. These are the mean diurnal temperature range (DTR), mean temperature of warmest quarter (TWmQ), precipitation of driest week (PDrWk), precipitation seasonality (PS), radiation of wettest quarter (RWeQ), radiation of warmest quarter (RWmQ), radiation of coldest quarter (RCQ) and mean annual moisture index (MI). A VIF value less than 4 was obtained for all the variables except in two cases i.e. RWmQ in the year 2100 for scenario A1B (>4.6) and scenario A2 (>5.7). The niche equivalency determined using the Maxent model showed that the two species occupy identical niches. The D values (0.657–0.661) and I values (0.872–0.891) derived using the niche similarity test were within 95% confidence intervals ($p = 0$).

3.2. Predicting climatic conditions of species

DTR value may vary by $\pm 0.37^\circ\text{C}$, with a mean drop of 0.35°C , in the distributional range of *C. tora* in the new climate, while there

could be a rise in TWmQ (minimum, 6.18°C ; maximum, 8.14°C ; mean, 7.4°C). PDrWk might fall by 2050 and rise by 2100 relative to the present climate, while PS may continue to rise till 2100 through 2050. The range of RWeQ in the distributional range of *C. tora* could expand by 10.6 W m^{-2} , with a marginal rise in the mean value (2.6 W m^{-2}) in the future climate. There could be a significant rise in the RWmQ minima of 48 W m^{-2} and a marginal rise in the maxima over 7 W m^{-2} , leading to a mean rise of 6 W m^{-2} in the distributional range of *C. tora* occurrence by 2100. *C. tora* may experience a decrease in RCQ and moisture availability in the future climate by 2100 (Table 1).

The minimum DTR may increase by 0.34°C , and the maximum value could decrease by 1.2°C , with a marginal drop in the mean value of 0.3°C in the distributional range of *L. camara* in the new climate. The mean TWmQ is likely to increase by 7°C with consistent rises in the minimum (5.7°C) and maximum (7.8°C) values in the distributional range of this species in the future climate. PDrWk might rise by 2050 and fall by 2100, with an overall decrease in the mean value in comparison with the present climate, while PS may continue to rise till 2100 through 2050. The mean RWeQ could fall marginally (4.2 W m^{-2}) despite rises in the minimum (ca. $8\text{--}11 \text{ W m}^{-2}$) and maximum values (9.8 W m^{-2}) in the distributional range of *L. camara* in the future climate. The mean RWmQ could expand by $2\text{--}6 \text{ W m}^{-2}$ owing to the substantial rise in the minimum values, which will be more significant in the year

Table 1

Descriptive statistics of climate variables for the current condition and for future scenarios (A1B and A2) of the years 2050 and 2100.

	Variables	Current			2050_A1B			2050_A2			2100_A1B			2100_A2		
		Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
<i>Cassia tora</i>	DTR	7.03	15.10	12.34	7.18	14.80	12.20	7.17	14.83	12.21	7.32	14.53	12.07	7.40	14.38	11.99
	TWmQ	4.56	33.79	31.52	7.09	36.91	34.48	6.89	36.67	34.25	9.45	40.08	37.33	10.74	41.93	38.92
	PDrWk	0.00	3.90	0.69	0.00	4.81	0.54	0.00	4.81	0.56	0.00	3.79	0.34	0.00	4.22	0.29
	PS	0.43	1.51	1.24	0.51	1.64	1.26	0.50	1.63	1.26	0.61	1.71	1.30	0.67	1.78	1.31
	RWeQ	131.56	234.77	174.40	139.36	225.69	176.16	138.55	225.75	176.06	141.63	224.85	176.90	141.94	224.39	177.04
	RWmQ	126.82	271.48	234.59	157.00	274.33	236.62	156.11	274.12	236.54	167.52	277.01	238.71	174.79	278.46	240.50
	RCQ	112.67	200.78	175.25	106.84	203.23	172.39	107.06	203.27	172.59	104.18	206.96	170.59	102.74	206.87	169.54
	MI	0.16	1.25	0.57	0.13	1.24	0.55	0.13	1.24	0.55	0.14	1.23	0.54	0.13	1.23	0.53
<i>Lantana camara</i>	DTR	6.74	15.56	11.57	6.88	15.06	11.55	6.87	15.10	11.55	7.02	14.60	11.54	7.08	14.35	11.53
	TWmQ	16.93	34.38	29.98	19.21	37.18	32.79	19.04	36.97	32.57	21.42	40.33	35.48	22.63	42.19	36.97
	PDrWk	0.00	6.04	1.18	0.00	7.34	1.03	0.00	7.34	1.07	0.00	6.43	0.47	0.00	6.43	0.40
	PS	0.49	1.51	1.05	0.60	1.48	1.11	0.59	1.47	1.10	0.63	1.67	1.19	0.63	1.75	1.22
	RWeQ	129.18	238.25	174.61	138.29	242.52	173.65	137.50	242.51	173.76	140.01	247.75	171.68	139.51	248.04	170.41
	RWmQ	126.13	264.25	226.86	146.15	264.44	228.95	145.23	264.44	228.76	163.08	264.73	231.43	170.27	266.00	233.06
	RCQ	115.60	202.25	173.28	110.70	203.43	171.41	110.92	203.47	171.54	107.93	207.14	170.22	106.43	207.09	169.38
	MI	0.17	1.90	0.63	0.17	1.88	0.61	0.17	1.88	0.61	0.18	1.85	0.59	0.18	1.83	0.58

Abbreviations: DTR = mean diurnal temperature range ($^\circ\text{C}$), TWmQ = mean temperature of warmest quarter ($^\circ\text{C}$), PDrWk = precipitation of driest week (mm), PS = precipitation seasonality (C of V), RWeQ = radiation of wettest quarter (W m^{-2}), RWmQ = radiation of warmest quarter (W m^{-2}), RCQ = radiation of coldest quarter (W m^{-2}), MI = annual mean moisture index.

The minimum DTR value would increase, and the maximum DTR value would fall in the distributional ranges of *C. tora* and *L. camara*. A higher mean DTR is expected in the locations of these species. The mean value of TWmQ would be higher in the distributional ranges of *C. tora* (31.5–38.9 °C) than that of *L. camara* (29.9–37.2 °C). The minimum value will be substantially lower (4.6–10.7 °C) in the distributional ranges of *C. tora* than of *L. camara* (16.9–22.6 °C). However, the maximum TWmQ value will be relatively same in the distributional ranges of *C. tora* (33.8–41.9 °C) and *L. camara* (34.4–42.2 °C). In general, PDrWk would decrease in their localities, more significantly in *L. camara* (1.18–0.4 mm) than in *C. tora* (0.69–0.29 mm). Overall, the mean PS value would increase in locations of both species in the future climate, with a higher range in the distributional range of *C. tora* (1.05–1.22) than that of *L. camara* (1.24–1.31). RWeQ would show similar variations, but with a greater range in the distributional range of *C. tora* than that of *L. camara*. RWMQ would rise in the distributional range of *L. camara* (226–233 W m⁻²) in the new climate. RCQ would show a marginal increase from the current condition to the forecasted scenarios, but with a high mean in places where *C. tora* occurs. The mean and the range of moisture availability will be greater in locations where *L. camara* occurs (0.59–0.63) compared with locations where *C. tora* occurs (0.53–0.57) (Table 1).

Central India may be suitable for *C. tora* in the future climate, while the northern, north-eastern, southern and western arid regions could be unsuitable. The Western Himalayas are predicted to be suitable for *C. tora* till 2050 but are likely to be unsuitable in 2100. The Western Ghats are less likely to be invaded whereas the major parts of the peninsular region could be unsuitable for *C. tora* (Fig. 2(a–e)). The chances of *L. camara* invading the Western Himalaya and the Western Ghats are high. *C. tora* is less likely to invade the coastal plains and the western arid regions of India (Fig. 2(f–j)).

The range size of *C. tora* is likely to expand by 5.8–10.4%, with an overall shift towards the outer boundaries of the current locations (Fig. 3(a–d)). Similarly, the range size could expand by 2–11.8% across the outer boundaries of the present locations, i.e., unfilled

3.5. Comparing SDMs

3.6. Contributions of the variables

The results of the jackknife test showed that the distributions of both *C. tora* and *L. camara* may be significantly attributed to solar radiation. RCQ has been the dominant contribution in explaining the distribution of species as its exclusion reduces model accuracy. RWmQ was found to be a significant factor the determination distribution, and its contribution showed a consistent increase temporally (Appendix S1). RWeQ was predicted to be highly significant in the distribution of *L. camara*, more so compared with *C. tora* (Appendix S2). The mean DTR was found to influence the distributions of both species, and could continue to do so more prominently for *L. camara* in the future climate. In contrast, TWmQ was predicted to have a consistent impact on the distribution of *L. camara*, and its influence on the distribution of *C. tora* in the future was found to increase. These variables appeared to preserve valuable information that is not found in other variables. PS made the greatest contribution to the distribution of *C. tora* in 2050. It was found to be the second-most predictor for *C. tora*, and its impact increased consistently from the current condition to 2100 through

Discriminatory abilities of models [generalised linear model (GLM), generalised additive model (GAM) and maximum entropy (Maxent)] for both un-calibrated (Uc_AUC) and calibrated (cAUC) conditions; The Uc_AUC conditions showed better predictive power with the Maxent model followed by GAM and GLM; The precision of the un-calibrated models was better compared with the calibrated models, but in certain cases the results were insignificant and below random (exceptions in bold).

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2050. Although PS would contribute higher in 2100, its significance would be less for the distribution of *L. camara* than for that of *C. tora*. The moisture availability could increasingly regulate distribution of both species in the new climate and from the moderate to extreme scenario of both 2050 and 2100. Even though the contribution of this variable was predicted to be low, it was found to preserve distinctive information for distribution, more significantly for *C. tora* than for *L. camara*. PDrWk was found to be the least significant predictor for distribution (Appendices S1 and S2).

3.7. Response curves

We focused on four variables that were found to contribute significantly in distributions of the two species. In general, the ranges of the environmental variables reduced with a marginal increase in the minima and decrease in the maxima. In *C. tora*, DTR was found to have two peaks, with a maximum between 7.5 °C and 9 °C, and another between 11.2 °C and 14.6 °C for the current condition. The peaks for the forecasted scenarios of 2050 and 2100 were almost within the same ranges. During the warmest quarter, *C. tora* was found to realise a narrow range of temperature (28–40 °C) in the current condition. The range reduced marginally in 2050 (31–42 °C). However, the temperature range was found to

increase between 27 °C and 40 °C for scenario A1B, and 29 °C and 43 °C for scenario A2 in 2100. The PS showed a positive unimodal relation with the distribution of *C. tora*, and the optimum value ranged between 0.7 and 0.18. The relationships between RCQ and species presence were multimodal, and the optimum ranged between 120 W m⁻² and 200 W m⁻² (Fig. 5). With *L. camara*, DTR showed a relatively unimodal pattern with species presence, with peaks between 8 °C and 13.5 °C. Its effect was more pronounced and consistent in 2050 than in 2100. On the other hand, TWmQ showed a similar curve pattern and its effect on this species was more significant with peaks between 25 °C and 40 °C. PS showed a positive correlation with species presence in the current condition. However, the variable was found to have a negative influence in the forecasted scenarios of 2050 and 2100. RCQ showed multimodal relationships with species presence, and the optimum ranged between 120 W m⁻² and 200 W m⁻² (Fig. 6).

4. Discussion

4.1. Impacts of climate change

In general, the distributions of *C. tora* and *L. camara* would significantly be constrained by solar radiation, which indicates that

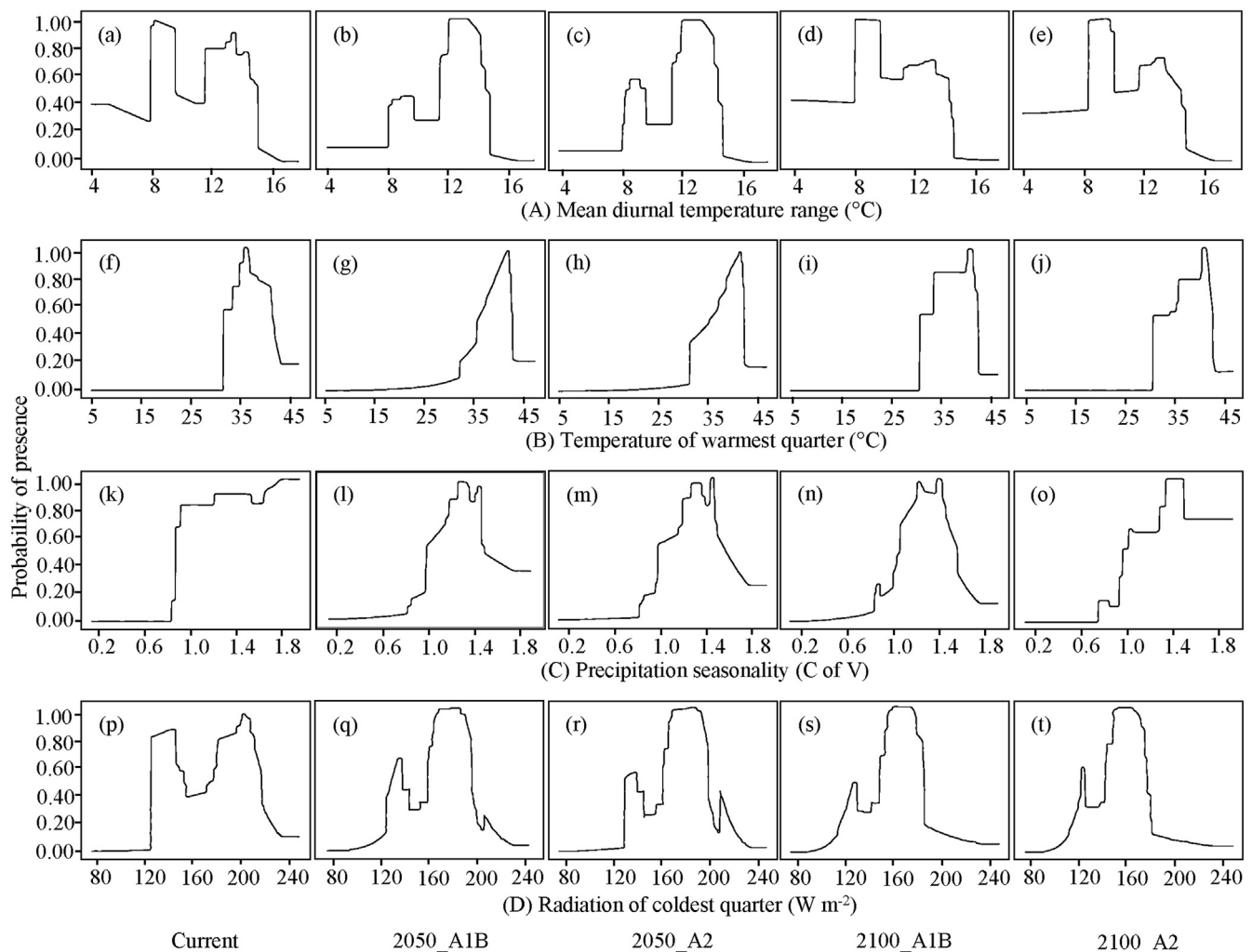


Fig. 5. Probability of presence of *Cassia tora* in response to (A) mean diurnal temperature range [a–e], (B) temperature of warmest quarter [i–j], (C) precipitation seasonality [k–o] and (D) radiation of the coldest quarter [p–t] for the current condition and climate change scenarios in the years 2050 and 2100. Overall, the impacts of climate change shift the optimum ranges of the variables.

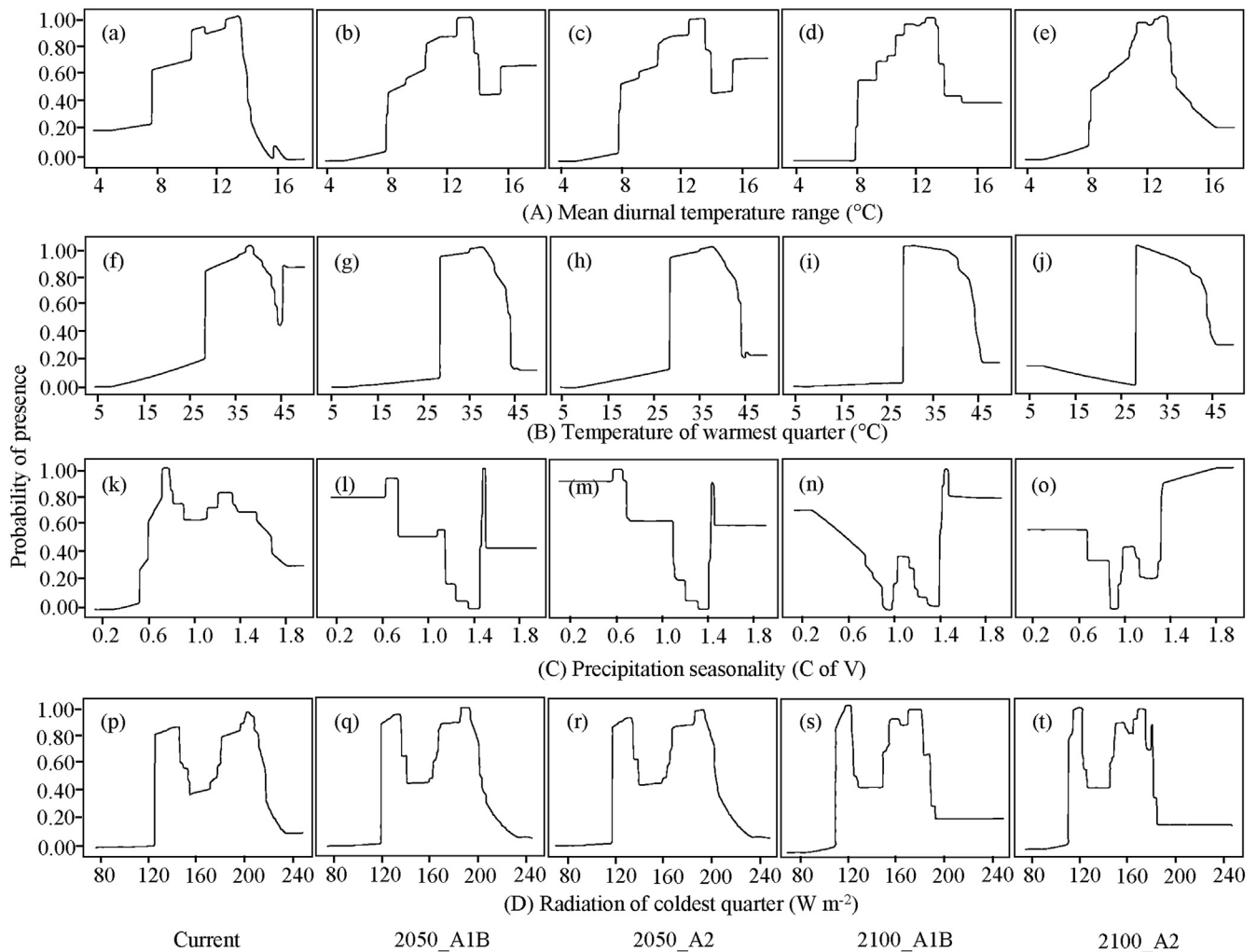


Fig. 6. Probability of presence of *Lantana camara* in response to (A) mean diurnal temperature range [a–e], (B) temperature of warmest quarter [f–j], (C) precipitation seasonality [k–o] and (D) radiation of the coldest quarter [p–t] for the current condition and climate change scenarios in the years 2050 and 2100. Overall, the impacts of climate change shift the optimum ranges of the variables.

irradiative surfaces and open spaces would favour their distribution. Bhagwat et al. (2012) reported that *L. camara* mostly occurs in urban areas, which demonstrates the significant influence of radiation on its distribution. Deforestation, clearance of canopy-cover, agriculture, fire and other anthropogenic interventions could further accelerate the invasion potential of the species (O'Donnell and Ignizio, 2012). The optimal radiation ranges during the coldest quarter of the two species are similar. This indicates that a minimum level of radiation is necessary to protect their seeds from low temperatures. Our results corroborate with the findings of Singh (1968) who reported that low-temperatures inhibit colonisation in *C. tora* by delaying seed germination. The capacity of the species to withstand tissue denaturing due to low temperatures would determine its colonising efficiency. *L. camara* was found to be more efficient at colonising compared with *C. tora* on account of its effective seed dormancy and high seed-yielding capability.

The mean diurnal temperature range shows a significant effect on the distribution of *C. tora*. This probably explains the high-energy demand of the species, which has an annual life cycle, for rapid physiological activities. This probably explains the greater significance of mean diurnal temperature above 0.14 °C in the distribution of *C. tora* than that in *L. camara*, indicating the importance of daily temperature range for annual species. Although

C. tora is found in places with broad temperature ranges, it would tolerate only a narrow temperature range, suggesting that it is sensitive to thermal stress. Its short life and fast growth probably help counter the negative impacts of high temperature maxima. Singh (1968) reported that warm climatic conditions favour the distribution of *C. tora* and that low-temperatures inhibit its colonisation by delaying seed germination. The mean diurnal temperature range would have a similar effect on the distribution of *L. camara*. However, its impact increases temporally from the current condition to the forecasted scenarios of 2050 and 2100. This is explained by the sensitivity of *L. camara* to rising temperatures. The temperature in the warmest quarter has a substantial impact on the distribution of *L. camara*. However, this species would flourish in marginally higher thermal ranges compared with *C. tora*. The higher temperature minima would favour the distribution of *L. camara*, while higher temperature maxima would restrict its distribution. This indicates the negative effect of the maximum temperature on the distribution of *L. camara* in the future climate. In extreme climate change scenario A2, both species are likely to be greatly affected by increased water demand. The consistent impact of DTR and increasing effect of TWmQ on the distribution of *C. tora* are exactly follow opposite pattern for *L. camara*, and thereby, could explain their complementarity in distribution. Such differences in

their thermal dependences may be ascribed to the differences in their phenological cycles, i.e., the significance of diurnal conditions for annual species and seasonal conditions for perennial species. Variations in precipitation pattern has a positive effect on *C. tora* and a negative effect on *L. camara*. This suggests that the precipitation pattern would have distinctive influences on plant species of different life cycles and indicates phenology is crucial for distribution.

4.2. Invasive potential

Both the species have likeliness to open spaces with high solar radiation. The distribution of *C. tora* is restricted to the central parts of India with intense agricultural activities. Singh (1968) reported the prevalence of *C. tora* along open lands and crop fields in South-East Asia and the south-west Pacific. *L. camara*, on the other hand, is wide spread in places of high anthropogenic disturbance. It is also been reported that *L. camara* is a common weed of dry forests, *Jhum* (slash-and-burn) fallows, and pastures (Sharma et al., 2005). Hiremath and Sundaram (2005) and Berry et al. (2011) had similar observations who advocated the invasion success of *L. camara* in disturbed habitats outcompeting native species. The availability of moisture is crucial for the distribution of *C. tora* as it occurs in places with high thermal ranges, with a narrow optimal temperature range. Its absence in the western regions with an arid climate and southern India indicates that extreme high temperature has a negative effect on its distribution. Its absence in the peninsular region may be attributed to the negative influence of soil salinity on its distribution (Fig. 1(a–e)). Similarly, *L. camara* would be avoiding the western arid regions, with an extremely dry and hot climate. Like *C. tora*, this species is absent in the south coastal plains, indicating that soil salinity has a negative effect on its growth and distribution (Fig. 1(f–j)). This corroborates with the findings of Swarbrick et al. (1998) who reported that salinity has deleterious effect on the distribution of *L. camara*. The chances of the two species invading the extreme northern and north-east regions of India are low. The low-temperatures and dense canopy architecture of these regions probably act as natural barriers to invasion.

The field observations (26 November to 2 December 2016) and (4–7 March 2017) confirms the accession of *L. camara* to open places of north-east India, i.e., Tripura. *C. tora* is found in isolated patches, and it is still to invade the most parts of the region. These findings corroborate the results of the predictions of models. Long-distance dispersal of *L. camara* by birds might have facilitated exploration of new areas. *C. tora* lags behind, being dispersed over short distances by water and animals. Parts of the Western Ghats would be highly infested by *C. tora*, indicating that it poses an invasion risk to this species-rich biodiversity hotspot. *L. camara*, in contrast, wide spread in some parts of Western Himalaya and the Western Ghats, posing threats to these biodiversity-rich regions. Earlier studies also have reported the invasion of *L. camara* in Pauri Garhwal region of the Himalayas (Dobhal et al., 2011), central India (Sahu and Singh, 2008), lower Siwalik Hills of Western Himalaya (Singh et al., 2014) and the Western Ghats (Sundaram and Hiremath, 2012).

4.3. Range size changes

Maxent predicts the distributions of both the invasive species with higher discriminatory ability compared with the regression models. Therefore, we used this model's predictions for further analysis. The range sizes show spatio-temporal variations in the future climate (Fig. 3). In general, the net changes in range size are positive owing to the expansion being greater than reduction. However, the magnitude of the range expansion decreases in 2100,

indicating the negative impact of climate change on species invasion beyond a thermal optimum. The slow rate of range expansion under climatic extremes explains the profound effect that water has on their distribution. The probability of range reduction in *L. camara* in the future climate has already been reported (Taylor and Kumar, 2013). The net range reduction of *C. tora* is less than that of *L. camara*. This shows that *C. tora* is highly successful in preserving niche space. Its limited ability to disperse might have restricted its expansion. *L. camara*, on other hand, would invade unfilled niche spaces and spread into unoccupied places. Its ability to disperse over long distances may be crucial for exploring new habitats. *L. camara*, with its greater seed-yielding capability and long-dispersal mechanisms, shows a greater ability to occupy unfilled niche spaces. Comparatively, *C. tora* has less efficient seed production and dispersal mechanisms, and, therefore, the distribution of this species is more or less localised.

Both the species occupy identical niches, and their peak productivity periods overlap. Therefore, *L. camara* might face competition for resources in places where it coexist with *C. tora*. It has been reported that *L. camara* competes with fast-growing annual species (Blank and Carmel, 2012). The seed production and germination potential of *L. camara* would facilitate its invasion. *L. camara* could avoid competition with *C. tora* by shifting habitats (Fig. 4). Earlier studies also have reported a significant shift in *L. camara*'s niche in India Gonçalves et al. (2014). It is suggested that the arrival times of these invasive species influenced their capacities to explore new niches. Thus the chances of occupying unfilled or potentially usable niches become available to the species that can utilise available resources efficiently (Cornell, 1999; Lekevičius, 2009). The invasion of annuals, with their higher rates of seed production, seed dormancy and efficient dispersal mechanisms, may be superior to that of perennials. However, within the same niche space, with perennials whose active growth phase overlaps that of annuals, the plants with the advantage of temporal complementarity would prevail over the competition. The differences in the phenological cycles of the plants would determine their invasion success. However, a species with better adaptability to adverse climatic conditions would have a competitive advantage over others, irrespective of phenological cycles.

4.4. Model comparison

Although the predictions of the models differ, an overall agreement was realised between the Maxent and regression models. All the models were found to identify PS and TWmQ as having significant roles in the distributions of *C. tora* and *L. camara*, respectively. In general, the impacts of solar radiation and moisture availability became significant with the rising temperatures in the future, more so in extreme forecasted scenarios. There was an overall agreement between the predictions of the Maxent model and GAM. This explains that the relationships between species and the environment are nonlinear. Both the regression models predicted that PDrWk would impact distribution significantly, in contrast with the predictions of the Maxent model. Maxent is the best parsimonious model, and its efficiency has been tested in predictions of invasive species distribution (Hoffman et al., 2008; Lemke and Brown, 2012; Kumar et al., 2015). Its ability to control over-fitting by regularisation and clamping and by retaining the same bias between the present and background points improves its discriminatory ability (Phillips et al., 2006). The smooth functions of an additive model could control over-fitting equivalent to regularisation. Both models are capable of fitting complex and nonlinear associations between species and the environment. On the other hand, the linear regression model is weak in explaining these complexities and predicted with a low discriminatory ability (Table 2).

5. Management implications

C. tora mostly affects the central regions of India, posing threats to agriculture. *L. camara* poses threats to the Western Himalaya and the Western Ghats, which are species-rich biodiversity hotspots. This indicates the possibility of crop damage by *C. tora* and alteration of native ecosystems by *L. camara*. Therefore, a well-designed management plan may provide some control against further invasion and the growing menace of these species in native ecosystems. We suggest that dense forest canopy cover be maintained by preserving dense forests to check invasion of these shadow-phobic species. Continued plantation may control their rapid colonisation in disturbed habitats with high irradiation and open-canopied land surfaces. Weeding may be recommended for *C. tora* before mid-September, when the plant is in its rapid growth phase. Since *L. camara* is capable to resist fire, continuous uprooting, at least twice a year, and consecutively for 3–4 years, will be useful in containing its colonisation. Public awareness regarding the possible threats posed by invasion, may encourage local people to preserve forest, which will ultimately control invasion. Involving local people would accelerate the process of eradication of these notorious weeds and conservation efforts. Ecologists, conservationists and nature-lovers should prioritise their efforts to control the menace of species invasion to biodiversity-rich native ecosystems. Policy-makers could have a key role in validating conservation measures early to check the spread of these species with rapid colonisation potential.

6. Conclusions

Invasive species may have unique responses to climate change with highly species-specific invasive potential. We took the advantage of an extensive floral database to assess the impacts of climate change on the distributions of *C. tora* and *L. camara* in the future. The study revealed that the distribution of *C. tora* (annual) and *L. camara* (perennial) would depend on the precipitation of the warmest quarter and moisture availability. The distribution of *C. tora* showed a narrow range of thermal tolerance, but one that is positively influenced by variability in precipitation pattern. Its presence in places where the moisture availability is low would negatively affect its distribution in the future climate. In contrast, *L. camara* is distributed in areas of high temperature minima and moderate moisture availability. The species displayed high thermal tolerance and could endure water stress under extreme climate change scenarios, which signify that it uses water instantly and efficiently. However, variations in precipitation patterns would have a deleterious effect on its distribution. In general, the two species were complementary in terms of dependence on climate, with the radiation of the coldest quarter playing a significant role. Although these species have distinct phenological cycles, climate change would favour the expansion of the ranges of both over space and time, and so there is a risk of their invading native ecosystems in the future. Notably, the invasion of *C. tora* would affect the agrarian economy and that of *L. camara* could pose a risk to the biodiversity-rich Himalaya and Western Ghats. The climatic variations in the future clearly define the possibility of temporal complementation of the distribution of the two species. Although the selected threshold might not be the true limit for suitability—unsuitability, the habitat suitability maps identify the potential threat areas crucial for an immediate action plan to check further spread, and help conservationists and planners make faster management prescriptions. However, the study is limited in its scope in comparing two species of contrasting habits. Addition of non-climatic factors may strengthen the findings.

Acknowledgements

The location information of the two species procured from Indian National Biodiversity Characterization at Landscape Level database is thankfully acknowledged. We acknowledge the anonymous reviewers for their comments that improved the quality of the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jenvman.2017.12.053>.

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